A morphometric analysis of *Arceuthobium campylopodum, A. laricis*, and *A. tsugense* (Viscaceae)

Robert L. Mathiasen
School of Forestry, Box 15018, Northern Arizona University, Flagstaff, Arizona 86011
Robert.Mathiasen@nau.edu

Shawn C. Kenaley
School of Integrative Plant Science, Plant Pathology and Plant-Microbe Biology Section,
Cornell University, Ithaca, New York 14853
sck26@cornell.edu

ABSTRACT

The classification of the dwarf mistletoes (*Arceuthobium* spp., Viscaceae) commonly parasitizing western hemlock (*Tsuga heterophylla*) and western larch (*Larix occidentalis*) in the northwestern United States and Canada has been one of the more difficult taxonomic problems associated with this important group of parasitic flowering plants. We collected new morphological measurements for the dwarf mistletoes parasitizing these commercially valuable conifers, *Arceuthobium tsugense* and *A. laricis*, respectively, from throughout most of their geographic ranges and used non-parametric univariate and multivariate statistical analyses to compare the morphological differences between them. In addition, because some investigators consider these taxa to be conspecific with, or subspecies of *A. campylopodum,* we included this dwarf mistletoe in our statistical analyses. Our analyses demonstrated that *A. tsugense* and *A. laricis* can be reliably segregated from each other, as well as from *A. campylopodum*, using plant heights, plant basal diameters, staminate spike widths, flower diameters, and fruit dimensions. Furthermore, their host affinities clearly distinguish them from each other. Therefore, we recommend they continue to be recognized as species. Morphological differences between these dwarf mistletoes are summarized and a key is provided for use in their identification. Published on-line www.phytologia.org *Phytologia 97(3): 200-218 (July 1, 2015).* ISSN 030319430.

KEY WORDS: *Arceuthobium* spp., Viscaceae , morphological characters, multivariate analyses, taxonomy, *Larix, Pinus*, *Tsuga.*

The dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are among the most damaging parasites of commercially valuable conifers in the western United States and Canada (Hawksworth et al. 2002). Two of the most economically important species are western hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) and larch dwarf mistletoe (*A. laricis* (Piper) St. John) because they cause mortality and significant growth loss of severely infected western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western larch (*Larix occidentalis* Nutt.), respectively (Hawksworth and Wiens 1996; Beatty et al. 1997; Hennon et al. 2001). Because these mistletoes are morphologically similar and flower and disperse seed at approximately the same time, their taxonomic classification has undergone many changes and is still under debate (Gill 1935; Hawksworth and Wiens 1972, 1996; Nickrent 2012).

The taxonomy of these dwarf mistletoe populations has become a topic of debate primarily because of recent molecular data (Nickrent et al. 2004). The molecular markers examined thus far indicate these taxa are very closely related to each other, as well as to *Arceuthobium campylopodum* Engelm., and therefore, their segregation from *A. campylopodum* as distinct species has been questioned (Nickrent et al. 2004; Baldwin et al. 2012). In addition, although the principal hosts of these dwarf mistletoes are distinct and represented by three different genera in the Pinaceae, these mistletoes also parasitize some of the same hosts. However, the susceptibility of their less commonly infected hosts varies considerably (Hawksworth and Wiens 1996; Mathiasen 1998; Mathiasen and Daugherty 2005).

In their first and since revised monograph of *Arceuthobium*, Hawksworth and Wiens (1972, 1996) recognized both *A. laricis* and *A. tsugense* as distinct species. Despite the morphological dissimilarities with *A. campylopodum* and the fact that *A. tsugense* does not parasitize *Pinus ponderosa* Douglas ex Lawson & C. Lawson or *P. jeffreyi* Grev. & Balf., the principal hosts of *A. campylopodum*, Nickrent et al. (2004) grouped *A. tsugense* under *A. campylopodum* based on molecular data. Furthermore, they grouped *A. laricis* under *A. campylopodum*, despite their morphological discontinuities and only occasional parasitism of *P. ponderosa* by *A. laricis*. The treatment for *Arceuthobium* by J. Kuijt in Baldwin et al. (2012) also grouped *A. tsugense* under *A. campylopodum*. These classifications have caused a good deal of uncertainty about the taxonomy of these economically and ecologically important dwarf mistletoes in the western United States and Canada, which has been further compounded by the recent recombination of *A. tsugense* and *A. laricis* as subspecies of *A. campylopodum* by Nickrent (2012).

We undertook this study because a detailed morphometric analysis comparing *Arceuthobium tsugense*, *A. laricis*, and *A. campylopodum* has not been completed. We collected a good deal of additional morphological data, far beyond the extent of that reported in Hawksworth and Wiens (1972, 1996) for *A. tsugense* (Wass and Mathiasen 2003), *A. campylopodum* (Mathiasen and Kenaley 2015), and *A. laricis* (reported here). This enabled us to compare the morphological characteristics of these three taxa using both a non-parametric univariate analysis and a more robust multivariate analysis using a relatively large data set. Our findings demonstrated that these species can readily be distinguished using many morphological characters and we have provided a key for use in their identification under field/laboratory conditions.

MATERIALS AND METHODS

The senior author and Mr. Ed Wass collected morphological data for 19 *Arceuthobium tsugense* populations distributed throughout most of its geographic range on *Tsuga heterophylla* in the United States and on Vancouver Island, British Columbia (Wass and Mathiasen 2003; Figure 1). We collected morphological data for *A. campylopodum* from 60 populations (30 each from *Pinus ponderosa* and *P. jeffreyi*) from throughout most of its geographic range (Mathiasen and Kenaley 2015; Figure 2). Lastly, we collected morphological data for *A. laricis* on *Larix occidentalis* from 32 populations distributed through most of its geographic range in the United States from 2011-2013 (Figure 3). Voucher specimens for *A. campylopodum* and *A. laricis* consisting of the mistletoe with host material were deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC), or the University of Arizona Herbarium, Tucson (ARIZ). Voucher and specific population data, including GPS coordinates, have been archived electronically in SEINet (Southwest Environmental Information Network 2015): http://swbiodiversity.org/portal/index.php). Voucher specimens of *A. tsugense* were deposited at the Pacific Research Centre, Canadian Department of Forestry, Victoria, B. C., Canada (DAVFP).

For each mistletoe population, 10–20 male and 10–20 female infections (infected branches) were collected separately and the dominant plant (largest plant) from each infection was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for the taxonomic classification of *Arceuthobium* taxa. The following morphological characters were measured: 1) height, basal diameter, third internode length and width, and color of male and female plants; 2) mature fruit length, width, and color; 3) seed length, width and color; 4) length and width of staminate spikes; 5) staminate flower diameters for 3- and 4-merous flowers; 6) length and width of staminate flower petals; and, 7) anther diameter and anther distance from the petal tip. Plant heights were measured to the nearest 0.1 cm and all other measurements were made to the nearest 0.1 mm.

Plants were usually measured within 12-h, but no later than 24-h after collection. Only plants that were still attached to their host's branch and were fully turgid were measured. Measurements were made using a digital caliper (Mitutoyo America Corp., Aurora, IL) and a 7X hand lens equipped with a micrometer (Bausch & Lomb, Bridgewater, NJ). The basal diameter of plants was measured at the point where the plant was attached to the host branch. The length and width of the third internode above the base of plants was included in our morphological analyses because these characters have been frequently reported for dwarf mistletoes and provide information on the relative size and thickness of male and female plants (Hawksworth and Wiens 1972, 1996; Mathiasen and Daugherty 2007, 2009a, 2009b, 2013; Mathiasen and Kenaley 2015). The length of the third internode was determined by measuring from the top of the second internode above the base of a plant to the top of the third internode, locations which are easily observed (see Figs. 2.1, 2.3, and 2.9 in Hawksworth and Wiens 1996). The width of the third internode was measured at its midpoint. Staminate spike and flower measurements were made during the peak of anthesis whereas fruit and seed measurements were made during the peak of seed dispersal. Sample sizes for most morphological characters measured varied among the three species sampled because of the number of populations sampled and the number of plants measured per population also varied. We purposely did not include samples of plants collected from hosts other than principal hosts for each dwarf mistletoe because there is some evidence that plants are smaller on less susceptible hosts (Mathiasen and Daugherty 2009b).

Statistical Analyses

We assessed whether values for morphological characters differed between and among species using Welch's *t* tests to accommodate unequal sample sizes and variances (Zimmerman 2004). Character differences between species were further assessed using the non-parametric Steel-Dwass, multiple comparison post hoc test ($\alpha = 0.05$). Standard and forward-stepwise quadratic discriminant function analyses (DFA) – powerful multivariate pattern-recognition methods – were also performed separately to determine whether female or male plants of *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense* can be delimited to species using only morphological characters (Quinn and Keough 2002). Discriminant function analyses classification compared actual species membership defined a priori via field diagnosis to predicted species memberships according to only continuous female (n= eight characters) or male morphologies (n= 10 characters). Separate DFAs for female and male plants were executed using equal prior probabilities for each species (25%) rather than proportional to their occurrences in the data set(s) as previous molecular phylogenetic analyses failed to resolve these taxa to separate species (Nickrent et al. 2004). Standardized correlation coefficients for morphological characters of female and male plants were also calculated to assess the contribution of each character to the discriminant function; thereby, providing the principal morphologies separating the dwarf mistletoes. Likewise, stepwise DFA was utilized to examine systematically the smallest number of morphological characteristics, female or male, resulting in the highest precision in species classification (%, actual/predicted). To do this, stepwise models were executed using equal prior probabilities and the sequential addition of morphological characters most-to-least correlated to the discriminant function. The full-model DFA was validated by resampling separately the original (complete) data set for female and male plants; selecting at random 50 complete records per species and re-performing the DFA using all morphological characteristics simultaneously. Non-parametric tests and DFAs were computed in JMP Pro 10 (SAS Institute, Cary, North Carolina, USA).

RESULTS

The mean heights of female and male plants of *Arceuthobium campylopodum* were significantly greater than *A. tsugense* and *A. laricis* and those of *A. tsugense* were significantly greater than those of *A. laricis* (Table 1). The mean basal diameters of female and male plants were also significantly different for all three taxa. The mean lengths of the third internodes of female plants was significantly different for all

three species, but the mean lengths of the third internode of male plants was not significantly different between *A. campylopodum* and *A. tsugense*. The third intermodal length for male plants of the latter taxa (*A. campylopodum* and *A. tsugense*), however, was significantly greater when compared to *A. laricis*. Although the mean widths of the third internodes of both male and female plants were significantly different between each species, the mean widths were similar for *A. tsugense* and *A. laricis* (1.6 and 1.7 mm, respectively) (Table 1). But the mean width of the third internode for *A. campylopodum* was greater (2.5 mm) than the latter two taxa. The staminate spikes of *A. campylopodum* were significantly longer on average than the other species, but those of *A. tsugense* and *A. laricis* were not significantly different (Table 1). The mean width of staminate spikes was significantly different between all three taxa, with those of *A. campylopodum* the largest and *A. tsugense* had the most slender staminate spikes.

The mean diameter of 3-merous flowers was significantly smaller for *Arceuthobium laricis* and similar for the other two species (Table 1). The mean diameter of 4-merous flowers was similar for *A. tsugense* and *A. laricis* and largest for *A. campylopodum*, but the mean diameters were all significantly different. The mean lengths of petals only varied by 0.1 mm between all three species, but the means were significantly different. The mean width of petals was widest for *A. campylopodum* and was significantly different than the mean petal width for the other two species, which were both 1.2 mm. Mean anther diameters only varied from 0.5-0.7 mm, but were significantly different among species. The mean distance of anthers from the tips of petals was greatest for *A. campylopodum* (0.6 mm) and it was significantly different from the means for the other taxa which were 0.5 mm.

Mean fruit length was larger for *Arceuthobium campylopodum* (5.4 mm) and although the mean fruit lengths were similar for *A. tsugense* and *A. laricis* (4.4 and 4.3 mm, respectively), they were significantly different (Table 1). The mean width of fruits was also larger for *A. campylopodum* (3.7 mm) while the means for the other species (2.9 and 3.0 mm) were not significantly different. The mean seed length was significantly different between all three species, and the seeds of *A. campylopodum* were larger (3.5 mm) as was the mean width of its seeds (1.5 mm). Although the mean width of the seeds for *A. tsugense* and *A. laricis* were similar (1.1 and 1.2 mm, respectively), they were significantly different. The principal characters that can be used to differentiate between *A. campylopodum*, *A. laricis*, and *A. tsugense* are summarized in Table 2.

Plant color is not usually an informative character for distinguishing between dwarf mistletoes. However, the color of plants of *A. laricis* was distinctly different from those of the other two species, being green-brown to reddish or almost purple. Plants of *A. tsugense* and *A. campylopodum* were predominantly yellow-green, green, or yellow-brown.

Separate quadratic discriminant function analyses (DFA) utilizing complete data for eight female and 10 male morphological characters (i.e., full-models) resulted in an overall correct classification rate of 94.3% (783/830) and 96.2% (982/1021), respectively (Table 3), and hence, readily separated *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense* according to species membership. Multivariate analysis of variance (MANOVA) indicated that the classification to predicted species of female (Wilks' λ= 0.1398, Approximant $F_{16,1640}$= 171.6, $P < 0.0001$; Pillai's Trace= 1.08, Approximant $F_{16, 1642}$= 120.2, $P < 0.0001$) and male plants (Wilks' λ= 0.1347, Approximant $F_{20, 2018}$= 174.0, $P < 0.0001$; Pillai's Trace= 1.17, Approximant $F_{20, 2020}$= 142.1, $P < 0.0001$) was significantly different from random. Means and associated 95% confidence intervals for morphological characters of female and male plants across predicted species according to full-model DFA are presented in Table 4.

Using the complete dataset and eight female characters, DFA correctly classified plants (predicted/actual) of *Arceuthobium campylopodum*, *A. laricis*, *A. tsugense* to species 97.7% (469/480), 92.0% (138/150), and 88.0% (176/200) of the time (Table 3), respectively, with the first discriminant function (canonical) explaining 91.9% of the total variation (Table 5). The latter taxon, *A. tsugense*, was

most often misclassified as *A. laricis* (8.5%; 17/150) and rarely to *A. campylopodum* (3.5%; 7/150) (Table 3). However, female plants diagnosed upon field identification as *A. laricis* were never delimited morpholgically to *A. campylopodum*, and vise versa, no specimens of *A. campylopodum* determined a priori were classified to *A. laricis*. Standardized correlation coefficients for DFA using the complete and resampled datasets, indicating the relative importance of individual female morphological characters in defining the discriminant functions, are listed in Table 6. Third internode length and width, seed length, and fruit length were most strongly correlated with the first and second canonical, and hence, contributed most to defining species membership when only female plants were considered. Using these four, female characters alone, the overall correct classification via DFA was 92.3% (766/830) with *A. campylopodum*, *A. laricis*, and *A. tsugense* classified correctly 97.1% (466/480), 92.0% (138/150), 81.0% (162/200) of the time, respectively (Table 3). The sequential addition of female morphologic characters (predicator variables) beyond those most correlated to the discriminant functions (female, steps 5-8, Table 3) only increased the correct classification rate for *A. tsugense* by seven percent to the maximum 88% and contributed little to further differentiate *A. tsugense* from *A. campylopodum* or *A. laricis* (Tables 3 and 6). Although female plants of *A. tsugense* were misclassified ≤ 8.5% of the time when eight morphological characters were considered (full-model), the multivariate mean and 95% confidence ellipse for this taxon – as well as *A. campylopodum* or *A. laricis* – did not intersect in multivariate space with those of the other taxa when analyses were executed with either the complete or resampled dataset (Figure 4).

Predicting species membership via DFA for male plants of *Arceuthobium laricis* and *A. tsugense,* was improved in comparison to DFA results for female plants, fruits, and seeds as an overall correct classification rate ≥ 97.3% was attained for both taxa using complete data and all 10 male characters (Table 3). The first and second discriminant functions described 84.7% and 15.3% of the variation among male plants (Table 5). Full-model DFA on male plants using complete or resampled data clearly differentiated all three taxa (Table 3; Figure 4). Analyses with complete data rarely misclassified *A. tsugense* as *A. laricis* (0.8%; 2/261) or *A. campylopodum* (1.9%; 5/261), and *A. laricis* was ascribed to *A. campylopodum* only 2.5% (4/160) of the time. Moreover, as demonstrated previously by DFAs of female plants, male plants identified in the field as *A. campylopodum* were also consistently and correctly classified as *A. campylopodum* (86.8-95.3%; 521-572/600) and were readily distinguishable from *A. laricis* and *A. tsugense* when considering as few as four morphological characters. Interestingly, DFA of male plants utilizing only two or three characters resulted in an overall correct classification rate of 92.3% (942/1021) or 91.6% (935/1021), respectively. Male morphology contributing greatest to the discrimination among *A. campylopodum*, *A. laricis*, and *A. tsugense* included third internode width, staminate spike width, anther diameter, third internode length, and anther distance from tip (Table 6), whereas, plant height, basal diameter, staminate spike length, and petal length and width contributed least to determining species membership. Male plant characters contributing most to the species discrimination were consistent between the complete and resampled datasets (Table 6), and the position of multivariate means across the three taxa in ordination space were maintained when comparing DFAs executed with either dataset (Figure 4).

DISCUSSION

Classifying *Arceuthobium tsugense* and *A. laricis* as conspecific or even subspecies of *A. campylopodum* is not supported by our analyses of the morphological characters we measured for these taxa. All three of these species can be reliably identified by differences in their plant heights, basal diameters, and width of their staminate spikes (Table 2). The mean widths of the third internode and the fruits and seeds of *A. campylopodum* were larger than those produced by the other taxa, which were about the same size. Characters that distinguished *A. laricis* from the other two species were its smaller male and female plants, its shorter third internode lengths, and smaller 3-merous flowers. Furthermore, although plant color is a qualitative character, *A. laricis* can be distinguished using plant color alone; it is typically green-brown, red, or purple.

The host range of *Arceuthobium tsugense* is distinct from both *A. campylopodum* and *A. laricis*; its principal host being *Tsuga heterophylla* and it does not parasitize *Pinus ponderosa* and *P. jeffreyi*, or *Larix occidentalis*, the principal hosts of *A. campylopodum* and *A. laricis*, respectively. Furthermore, *T. heterophylla* is very rarely infected by *A. laricis* (Hawksworth 1987) and is probably immune to infection by *A. campylopodum*. Because *T. heterophylla* and *P. ponderosa* are seldom sympatric, the latter host-mistletoe combination has not yet been verified (Hawksworth and Wiens 1996; Mathiasen and Daugherty 2005). Although *A. laricis* has been reported to parasitize *P. ponderosa*, it only occasionally infects this host in stands where it is also parasitizing *L. occidentalis* (Hawksworth and Wiens 1996; Mathiasen 1998). Likewise, although *Tsuga mertensiana* is considered a secondary host for *A. laricis* (Mathiasen 1998), this host is only occasionally parasitized by *A. tsugense* (Shaw 1982; Mathiasen and Daugherty 2005). While the susceptibility of *T. mertensiana* to *A. campylopodum* remains unknown, it is probably not susceptible.

Although *Abies amabilis* has been artificially inoculated successfully with *Arceuthobium laricis* (Smith and Wass 1972), this host is only rarely infected by *A. laricis* in Washington (Mathiasen et al. 1995). Therefore, although some of the same hosts are infected by both *A. laricis* and *A. tsugense*, the susceptibility of the hosts they have in common varies considerably (Table 2). None of the dwarf mistletoes share a principal host in common and the principal host of *A. tsugense* (*Tsuga heterophylla*) has only been reported to be infected by *A. laricis* from one location in Washington (Hawksworth 1987). Furthermore, *A. campylopodum* has never been reported naturally parasitizing a species of *Tsuga* or *Larix*. The host ranges of these dwarf mistletoes is further evidence they are genetically distinct and should be given separate taxonomic status. These three dwarf mistletoes clearly have very different host ranges and hence, their pathological significance in forests of the northwestern United States and Canada is also distinct. Furthermore, because their host ranges are so remarkably different, any efforts to manage populations of these parasites to mitigate their potential for causing growth loss and mortality of severely infected trees, must consider these differences (Hawksworth and Wiens 1996).

Some treatments of *Arceuthobium tsugense* now segregate this taxon into four subspecies based on morphology, phenology, geographic distribution, and host specialization (Hawksworth et al. 1992; Hawksworth and Wiens 1996; Wass and Mathiasen 2003; Mathiasen and Daugherty 2007). Because the morphological and host affinities of the subspecies have already been outlined in this literature, we only compared the morphological characteristics of *A. tsugense* subsp. *tsugense* with those of *A. laricis* and *A. campylopodum* in this study. It should be noted that although *Tsuga mertensiana* is a secondary host of *A. laricis* and a principal host of *A. tsugense* (Rosendahl) G. N. Jones subsp. *mertensianae* Hawksw., Wiens, & Nickrent, these dwarf mistletoes are morphologically distinct and geographically isolated from each other (Hawksworth et al. 1992; Hawksworth and Wiens 1996). Although, *A. tsugense* subsp. *mertensianae* has been reported from central and northern Oregon, Washington, and southern British Columbia (Hawksworth et al. 1992; Hawksworth and Wiens 1996), it is now known that these populations are based on parasitism of *T. mertensiana* by *A. tsugense* subsp. *amabilae* in central and northern Oregon (Mathiasen and Daugherty 2007) and by *A. laricis* in Washington and British Columbia (Mathiasen unpublished data).

Nickrent (2012) proposed that taxa within section *Campylopoda* Hawksw. & Wiens, series *Campylopoda* conform to the concept of ecotypes. He based his conclusion on the fact that because seeds of *Arceuthobium campylopodum* collected from one host tree may not survive on another host, species in series *Campylopoda* would best be represented as ecotypes since the most important environmental component affecting dwarf mistletoe survival and reproduction was the host tree. He contended that host specificity was not common for dwarf mistletoes because several of the subspecies he recognized have four principal hosts and parasitism of occasional and rare hosts overlaps between species. In reality, only *A. cyanocarpum* (sensu stricto) has four principal hosts, all closely related white pines (Hawksworth and Wiens 1996). Nickrent's (2012) summary of principal hosts for his subspecies of *A. campylopodum* was

based on his grouping of several taxa we recognize as subspecies of *A. abietinum*, *A. microcarpum*, and *A. tsugense*. This greatly skewed his principal host totals and misrepresented the actual host specificity of these three species. Following our interpretation of the subspecific classification of these species, none of them has more than two principal hosts. In addition, Nickrent's discussion of host specificity did not consider the severity of infection observed for secondary, occasional, or rare hosts or the fact that in many cases few mistletoes shoots are produced on occasional and particularly rare hosts; thereby indicating that many of the cases of dwarf mistletoe infection on less susceptible hosts are what Hawksworth and Wiens (1996) termed "incompatible." Furthermore, Nickrent (2012) did not discuss the importance of immune hosts and why this must also be considered when assessing the significance of host affinities and the taxonomic classification of dwarf mistletoes.

When dwarf mistletoe-host relationships are compared to other mistletoes, dwarf mistletoes are relatively host specific because many species, including the species studied here, only infect one or two species as principal hosts. Host preferences are indications of genetic differences between dwarf mistletoes and the greater the differences in the host's taxonomic relationships for principal as well as immune hosts, the greater the genetic differences between the dwarf mistletoes that preferentially infect or will not infect hosts which are phylogenetically closely related or unrelated (Hawksworth 1990). Furthermore, other investigators have demonstrated the large differences in the host affinities of the dwarf mistletoes studied here (Hawksworth and Wiens 1972, 1996; Mathiasen 1994, 1998; Mathiasen and Daugherty 2005). Obviously, we disagree with Nickrent's (2012) assertion that dwarf mistletoes are not host specific parasitic plants simply because they sometimes have more than one principal host and infect other species to varying degrees. In contrast, we consider dwarf mistletoe-host relationships to be critical in their taxonomic classification. Accordingly, we support the classification of dwarf mistletoe populations as species that primarily parasitize unrelated host genera such as *Pinus*, *Tsuga*, and *Larix* as principal hosts.

Nickrent (2012) also argued that since the range in plant dimensions (height, basal diameter, third internode dimensions) overlapped, had similar ITS and chloroplast DNA sequences, and that several species were sympatric, all of the members of series *Campylopoda* should be treated as subspecies of *A. campylopodum*. It is important to note that Nickrent (2012) concluded that there were adequate morphological and physiological differences between the species in series *Campylopoda* to warrant their at least having subspecific status under *A. campylopodum*. This was a major modification of his earlier recommendation that all the taxa in series *Campylopoda*, except *A. blumeri* A. Nelson, were conspecific (Nickrent et al. 2004). Our results have clearly demonstrated using statistical analyses of the many morphological characters we examined that *A. tsugense* and *A. laricis* are morphologically distinct from each other and even more so from *A. campylopodum*.

Considering the morphological data presented herein for *Arceuthobium campylopodum*, *A. tsugense,* and *A. laricis* and evident discontinuities in the host affinities among these taxa, we maintain that it is more consistent with other specific classifications of dwarf mistletoe populations to continue classifying these taxa as species. Recognition of the host affinities developed by dwarf mistletoes is critical in their classification because we consider differences in host preference(s) to reflect corresponding and underlying genetic differentiation between dwarf mistletoes. Our morphological analyses demonstrated that these species are readily separated using several characters (Table 2; Figure 4) and field observations of their host affinities have also demonstrated that they are genetically distinct in that they parasitize taxonomically distinct members of the Pinaceae as their principal hosts and only infect closely related conifers to a lesser degree.

KEY FOR IDENTIFICATION OF *ARCEUTHOBIUM LARICIS*, *A. TSUGENSE*, AND *A. CAMPYLOPODUM*

1. Plants green-brown, reddish, or purple, plants heights usually less than 6 cm; basal diameters usually less than 2.5 mm; 3-merous flowers less than 3 mm in diameter; primarily parasitic on *Larix occidentalis*, *Pinus contorta*, or *Tsuga mertensiana* ..... *Arceuthobium laricis*

1'. Plants yellow-brown, yellow-green, green, or brown at their base; plant heights usually greater than 6 cm; basal diameters usually greater than 2.5 mm; 3-merous flowers greater than 3 mm in diameter; primarily parasitic on *Pinus ponderosa*, *P. jeffreyi*, or *Tsuga heterophylla*..... 2

2. Plant heights usually less than 9 cm; basal diameters usually less than 3 mm; width of third internode usually less than 2 mm; staminate spike width usually less than 2 mm; mature fruits less than 5 mm long and 3 mm wide; seeds about 2.5 x 1.1 mm; primarily parasitic on *Tsuga heterophylla*..... *Arceuthobium tsugense*

2'. Plant heights usually greater than 9 cm; basal diameters usually greater than 3 mm; width of third internode usually greater than 2 mm; staminate spike width usually greater than 2 mm; mature fruits typically greater than 5 mm long and 3 mm wide; seeds about 3.5 x 1.5 mm; primarily parasitic on *Pinus ponderosa* and *P . jeffreyi*; also common on *P. attenuata* and *P. coulteri* ..... *Arceuthobium campylopodum*

ACKNOWLEDGEMENTS

The assistance of Dr. Carolyn M. Daugherty with morphological measurements and a review of the original manuscript are greatly appreciated. We also acknowledge the suggestions of two anonymous reviewers which greatly improved the final version of the manuscript.

LITERATURE CITED

Baldwin, B. G., D. Goldman, D. J. Keil, R. Patterson, T. J. Rosatii, and D. H. Wilken (editors). 2012. The Jepson Manual: Vascular Plants of California. Second Edition. University of California Press, Berkeley.

Beatty, J. S., G. M. Filip, and R. L. Mathiasen. 1997. Larch dwarf mistletoe. Forest Insect and Disease Leaflet 169, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Gill, L. S. 1935. *Arceuthobium* in the United States. Connecticut Academy of Arts and Science Transactions 32: 111–245.

Hawksworth, F. G. 1987. Taxonomy of hemlock dwarf mistletoe. *In* S. J. Cooley (editor), Proceedings of the 34th Western International Forest Disease Work Conference. USDA Forest Service, Forest Health Management, Portland, OR. Pp. 45-46.

Hawksworth, F. G. 1990. Coevolution of Mexican white pines and their dwarf mistletoe parasites. Pp 23-28 *in* Proceedings of a symposium on white pine provenances and breeding. General Technical Report NE-155. USDA Forest Service, Northeastern Forest Experimental Station, Radnor, PA.

Hawksworth, F. G., and D. Wiens. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agriculture Handbook 401, USDA Forest Service, Washington, DC.

Hawksworth, F. G., and D. Wiens. 1996. Dwarf mistletoes: biology, pathology, and systematics. Agriculture Handbook 709, USDA Forest Service, Washington, DC.

Hawksworth, F. G., D. Wiens, and D. L. Nickrent. 1992. New western North American taxa of *Arceuthobium* (Viscaceae). Novon 2: 204-211.

Hawksworth, F. G., D. Wiens, and B. W. Geils. 2002. *Arceuthobium* in North America. *In* B. W. Geils, J. Cibrian-Tovar, and B. Moody (editors), Mistletoes of North American Conifers. USDA Forest Service General Technical Report RMRS-GTR-98, Rocky Mountain Research Station, Ogden, Utah. Pp. 29-56.

Hennon, P. E., J. S. Beatty, and D. Hildebrand. 2001. Hemlock dwarf mistletoe. Forest Insect and Disease Leaflet 135, USDA Forest Service, Pacific Northwest Region, Portland, OR.

Mathiasen, R. L. 1994. Natural infection of new hosts by hemlock dwarf mistletoe. USDA Forest Service, Research Note RM-RN-530, Rocky Mountain Research Station, Ft. Collins, CO.

Mathiasen, R. L. 1998. Comparative susceptibility of conifers to larch dwarf mistletoe based on natural infection in the Pacific Northwest. Forest Science 44: 559-568.

Mathiasen, R. L., J. S. Beatty, and D. Hildebrand. 1995. First report of larch dwarf mistletoe on Pacific silver fir and on mountain hemlock in the Cascade Mountains, WA. Plant Disease 79: 1249.

Mathiasen, R. L., and C. M. Daugherty. 2005. Susceptibility of conifers to western hemlock dwarf mistletoe in the Cascade Range of Washington and Oregon. Western Journal of Applied Forestry 20: 94-100.

Mathiasen, R. L., and C. M. Daugherty. 2007. *Arceuthobium tsugense* subsp. *amabilae*, a new subspecies of hemlock dwarf mistletoe (Viscaceae) from Oregon. Novon 17: 222-227.

Mathiasen, R. L., and C. M. Daugherty. 2009a. *Arceuthobium abietinum* subspecies *wiensii*, a new subspecies of fir dwarf mistletoe (Viscaceae) from northern California and southern Oregon. Madroño 56: 118-126.

Mathiasen, R. L., and C. M. Daugherty. 2009b. Additional morphological measurements of *Arceuthobium siskiyouense* and *A. monticola* (Viscaceae). Journal of the Botanical Research Institute of Texas 3: 741-749.

Mathiasen, R. L., and C. M. Daugherty. 2013. Additional morphological measurements of *Arceuthobium littorum* and *A. occidentale* (Viscaceae). Phytologia 95: 70-78.

Mathiasen, R. L., and S. C. Kenaley. 2015. A morphometric analysis of dwarf mistletoes in the *Arceuthobium campylopodum-occidentale* complex (Viscaceae). Madroño 62: 1-20.

Nickrent, D. L., M. A. García, M. P. Martín, and R. L. Mathiasen. 2004. A phylogeny of all species of *Arceuthobium* (Viscaceae) using nuclear and chloroplast DNA sequences. American Journal of Botany 91: 125-138.

Nickrent, D. L. 2012. Justification for subspecies in *Arceuthobium campylopodum* (Viscaceae). Phytoneuron 51: 1-11.

Quinn, G. P., and M. J. Keough. 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Shaw, C. G., III. 1982. Mountain hemlock is occasional host for hemlock dwarf mistletoe in Alaska. Plant Disease 66: 852-856.

Smith, R. B., and E. F. Wass. 1972. Infection of *amabilis* fir by larch dwarf mistletoe. Canadian Department of Forestry, Bi-Monthly Research Notes 28 (1-2): 17.

Southwest Environmental Information Network. 2015. Available on-line at http://swbiodiversity.org/portal/index.php. (accessed 15 January 2015).

Wass, E. F., and R. L. Mathiasen. 2003. A new subspecies of hemlock dwarf mistletoe (*Arceuthobium tsugense* subsp. *contortae*, Viscaceae) from British Columbia and Washington. Novon 13: 268-276.

Zimmerman, D. W. 2004. A note on preliminary tests of equality of variances. British Journal of Mathematical and Statistical Psychology 57: 173-181.

Table 1. Morphological measurements for *Arceuthobium campylopodum*, *A. tsugense*, and *A. laricis*. Data are listed as **mean**, (SD) [n]. Means followed by different superscripted letters in the same row were significantly different using Welch's *t* tests and the nonparametric Steel-Dwass, multiple comparison post hoc test ($\alpha = 0.05$). Lower case letters in the brackets designate sample sizes already listed in the same column. Plant heights are in cm and all other measurements in mm.

Character	***Arceuthobium campylopodum***	***Arceuthobium laricis***	***Arceuthobium tsugense***
Plant height			
Female	**10.4**^{a} (2.7) [600a]	**5.3**^{b} (1.3) [160a]	**7.8**^{c} (2.2) [270a]
Male	**9.7**^{a} (3.0) [a]	**4.7**^{b} (1.3) [a]	**8.0**^{c} (2.0) [265b]
Basal diameter			
Female	**3.4**^{a} (0.7) [a]	**2.4**^{b} (0.5) [a]	**2.7**^{c} (0.8) [a]
Male	**3.2**^{a} (0.6) [a]	**2.1**^{b} (0.5) [a]	**2.6**^{c} (0.5) [b]
Third internode length			
Female	**13.0**^{a} (3.1) [a]	**8.5**^{b} (2.0) [a]	**12.3**^{c} (3.2) [a]
Male	**12.0**^{a} (3.3) [a]	**7.5**^{b} (1.9) [a]	**11.8**^{a} (3.3) [b]
Third internode width			
Female	**2.5**^{a} (0.4) [a]	**1.7**^{b} (0.2) [a]	**1.6**^{c} (0.4) [a]
Male	**2.5**^{a} (0.4) [a]	**1.7**^{b} (0.2) [a]	**1.6**^{c} (0.3) [b]
Staminate spike length	**12.7**^{a} (4.8) [760b]	**10.1**^{b} (3.1) [240b]	**10.8**^{b} (2.7)[260c]
Staminate spike width	**3.0**^{a} (0.3) [b]	**2.6**^{b} (0.2) [b]	**1.6**^{c} (0.1) [c]
Flower diameter			
3-merous	**3.1**^{a} (0.4) [400]	**2.7**^{b} (0.3) [120c]	**3.2**^{a} (0.5) [115d]
4-merous	**4.2**^{a} (0.5) [360]	**3.7**^{b} (0.3) [c]	**3.8**^{c} (0.5) [d]
Petal lobe length	**1.6**^{a} (0.2) [b]	**1.4**^{b} (0.2) [b]	**1.5**^{c} (0.2) [c]
Petal lobe width	**1.4**^{a} (0.2) [b]	**1.2**^{b} (0.2) [b]	**1.2**^{c} (0.2) [c]
Anther diameter	**0.6**^{a} (0.1) [b]	**0.5**^{b} (0.1) [b]	**0.7**^{c} (0.1) [c]
Anther distance from tip	**0.6**^{a} (0.1) [b]	**0.5**^{b} (0.1) [b]	**0.5**^{b} (0.2) [c]
Fruit length	**5.4**^{a} (0.5) [480c]	**4.3**^{b} (0.4) [150d]	**4.4**^{c} (0.4) [210e]
Fruit Width	**3.7**^{a} (0.4) [c]	**3.0**^{b} (0.3) [d]	**2.9**^{b} (0.2) [e]
Seed length	**3.5**^{a} (0.4) [c]	**2.4**^{b} (0.3) [d]	**2.6**^{c} (0.3) [200f]
Seed width	**1.5**^{a} (0.2) [c]	**1.2**^{b} (0.1) [d]	**1.1**^{c} (0.1) [f]

Table 2. Summary of the principal characters separating *Arceuthobium campylopodum*, *A. tsugense*, and *A. laricis*. Data for morphological characters are means; plant heights in cm and all other measurements in mm. Numbers in bold represent key morphological or phenological differences between the taxa. Host susceptibility classification based on information in Hawksworth (1987), Hawksworth and Wiens (1996), Mathiasen (1998), and Mathiasen and Daugherty (2005, 2007).

Character		***Arceuthobium campylopodum***	***Arceuthobium laricis***	***Arceuthobium tsugense***
Plant height				
	Female	**10.4**	**5.3**	**8**
	Male	**9.7**	**4.7**	**7.8**
Plant color		Yellow-green, green, yellow-brown	Brown-green, red, purple	Yellow-green, green, yellow-brown
Basal diameter				
	Female	**3.4**	**2.4**	**2.7**
	Male	**3.2**	**2.1**	**2.6**
Third internode width				
	Female	**2.5**	1.7	1.6
	Male	**2.5**	1.7	1.6
Staminate spike width		**3.1**	**2.6**	**1.6**
Flower diameter				
	3-merous	3.1	**2.7**	3.2
	4-merous	**4.2**	3.7	3.8
Fruit length		**5.4**	4.3	4.4
Fruit width		**3.7**	3	2.9
Sympatry among taxa		*A. laricis*	*A. campylopodum*	Not sympatric
Host Susceptibility				
	Principal	*Pinus jeffreyi*; *P. ponderosa*	*Larix occidentalis*	*Tsuga heterophylla*
	Secondary	*P. attenuata*; *P. coulteri*	*Tsuga mertensiana*; *P. contorta var. latifolia*	None
	Occasional	*P. contorta* var. *murrayana*, var. *latifolia; P. sabiniana*	*Abies lasiocarpa*; *Pinus ponderosa*	*Abies amabilis; A. grandis*; *A.procera; Pinus contorta var.latifolia; Tsuga mertensiana*
	Rare	*P. lambertiana*	*Abies grandis*; *Picea engelmannii; Pinus albicaulis; P. monticola; Tsuga heterophylla*	*Picea engelmannii*; *P. sitchensis; Pinus monticola; Pseudotsuga menziesii*
	Immune	*Abies grandis*		*P. contorta* var. *murrayana*

Table 3. Predicted taxonomic membership according to forward, stepwise discriminant function analyses (DFA) for the morphological classification of female (n= 8 characters) and male plants (n= 10 characters) using complete data. Correct classification (%, predicted/actual) per species-taxon membership combination greater than 90% are ar in **boldface**. Anther diameter (AD); anther distance from tip (ADT); basal diameter (BA); fruit length (FL); fruit width (FW); petal length (PL); petal width (PW); plant height (PH); staminate spike length (SSL); staminate spike width (SSW); third internode length (TIL); and, third internode width (TIW). Sample size (n; female, male plants): *Arceuthobium campylopodum* (480, 600), *A. laricis* (150, 160), and *A. tsugense* (200, 261).

Stepwise DFA (Step [Character])	**Species by predicted taxonomic membership (%, predicted/actual)**									
	Total	*A. campylopodum* (*Ac*)			*A. laricis* (*Al*)			*A. tsugense* (*At*)		
		Ac	*Al*	*At*	*Ac*	*Al*	*At*	*Ac*	*Al*	*At*
Female (n = 830 total plants)										
1. [**SL**]	71.1	80	2.3	17.7	2.7	74.7	22.7	6.5	46.5	47
2. [SL], [**TIW**]	84.3	94.8	0.4	4.8	1.3	78	20.7	7	29	64
3. [SL], [TIW], [**TIL**]	90.7	**95.6**	1	3.3	1.3	**90.0**	8.7	7	13.5	79.5
4. [SL], [TIW], [TIL], [**FL**]	92.3	**97.1**	0.8	2.1	0.7	**92.6**	6.7	5.5	13.5	81
5. [SL], [TIW], [TIL], [FL], [**SL**]	92.9	**97.1**	0.6	2.3	1.3	**91.3**	7.3	5	11	84
6. [SL], [TIW], [TIL], [FL], [SL], [**PH**]	94.2	**97.7**	0	2.3	0	**92.7**	7.3	4.5	8.5	87
7. [SL], [TIW], [TIL], [FL], [SW], [PH], [**FW**]	94.3	**97.7**	0	2.3	0	**93.3**	6.7	4	9	87
8. [SL], [TIW], [TIL], [FL], [SW], [PH], [FW], **[BD]**	94.3	**97.7**	0	2.3	**0**	**92.0**	8	3.5	8.5	88
Male (n = 1021 total plants)										
1. [**TIW**]	74.4	86.8	13	0.2	5.6	85.0	9.4	5.7	54.8	39.5
2. [TIW], [**SSW**]	92.3	**92.2**	6.8	1	3.8	**94.4**	1.9	4.6	4.2	**91.2**
3. [TIW], [SSW], [**AD**]	91.6	**91.3**	7	1.7	3.8	**91.3**	5	4.2	3.4	**92.3**
4. [TIW], [SSW], [AD], [**TIL**]	94.1	**93.2**	5.2	1.7	3.1	**96.3**	0.6	3.1	1.9	**95.0**
5. [TIW], [SSW], [AD], [TIL], [**ADT**]	94.9	**93.7**	5.3	1	3.1	**96.3**	0.6	1.5	1.5	**96.9**
6. [TIW], [SSW], [AD], [TIL], [ADT], [**PH**]	95.7	**94.3**	4.3	1.3	1.3	**97.5**	1.3	1.5	0.8	**97.7**
7. [TIW], [SSW], [AD], [TIL], [ADT], [PL], [**BA**]	95.6	**94.5**	4.3	0.8	1.9	**96.9**	1.3	1.9	0.8	**97.3**
8. [TIW], [SSW], [AD], [TIL], [ADT], [PL], [BA], [**SSL**]	96.2	**95.3**	3.7	1	1.3	**97.5**	1.3	1.9	0.8	**97.3**
9. [TIW], [SSW], [AD], [TIL], [ADT], [PL], [BA], [SSL], [**PW**]	95.9	**94.5**	4.3	1.2	1.9	**98.1**	0	1.5	0.8	**97.7**
10. [TIW], [SSW], [AD], [TIL], [ADT], [PL], [BA], [SSL], [PW], [**PL**]	96.2	**95.3**	3.7	1	2.5	**97.5**	0	1.9	0.8	**97.3**

Table 4. Quadratic discriminant function analyses (DFA) of male and female plants using complete data for *Arceuthobium campylopodum*, *A. laricis*, and *A. tusgense*. Comparison of morphological characters (means) according to predicted classification to species. Ninety-five percent confidence intervals (±) were computed for comparison of mean differences. Mean plant heights in cm and all other measurements in mm.

Character		***A. campylopodum***	***A. laricis***	***A. tsugense***
Plant height				
	Female	10.3 (±0.24)	5.6 (±0.21)	8.1 (±0.31)
	Male	9.8 (±0.24)	4.8 (±0.19)	7.8 (±0.27)
Basal diameter				
	Female	3.4 (±0.06)	2.4 (±0.07)	2.5 (±0.10)
	Male	3.2 (±0.03)	2.2 (±0.07)	2.6 (±0.08)
Third internode length				
	Female	13.1 (±0.27)	8.7 (±0.30)	12.9 (±0.49)
	Male	12.0 (±0.27)	7.7 (±0.28)	11.8 (±0.39)
Third internode width				
	Female	2.5 (±0.03)	1.7 (±0.04)	1.5 (±0.05)
	Male	2.5 (±0.03)	1.7 (±0.03)	1.6 (±0.04)
Staminate spike length		12.9 (±0.41)	10.1 (±0.43)	10.8 (±0.43)
Staminate spike width		3.0 (±0.02)	2.6 (±0.03)	1.6 (±0.12)
Anther diameter		0.6 (±0.01)	0.5 (±0.01)	0.7 (±0.02)
Anther distance from tip		0.6 (±0.01)	0.5 (±0.02)	0.5 (±0.03)
Petal length		1.5 (±0.02)	1.4 (±0.02)	1.5 (±0.03)
Petal width		1.4 (±0.02)	1.2 (±0.03)	1.2 (±0.02)
Fruit length		5.4 (±0.04)	4.3 (±0.06)	4.5 (±0.05)
Fruit width		3.7 (±0.04)	3.0 (±0.04)	3.0 (±0.03)
Seed length		3.5 (±0.04)	2.4 (±0.04)	2.6 (±0.04)
Seed width		1.5 (±0.03)	1.1 (±0.02)	1.1 (±0.02)

Table 5. Canonical statistics: quadratic discriminant function analysis (DFA) of female (n= 8 morphological characters) and male plants (n= 10 morphological characters) using complete data or randomly selected records (n= 50 complete records/taxon) for *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense*. Can = Canonical, Cum % = cumulative %, Canonical r = canonical correlation, L Ratio = likelihood ratio,

Sex / Sample	**Can**	**Eigenvalue**	**%**	**Cum %**	**Canonical r**	**L Ratio**	**Approx *F***	***P*-value**
Female								
Complete	1	4.22	91.9	91.9	0.9	0.14	$F_{16, 1640} = 171.6$	< 0.0001
	2	0.37	8.1	100	0.52	0.73	$F_{7, 821} = 43.4$	< 0.0001
Random	1	4.24	83.3	83.3	0.9	0.1	$F_{16, 280} = 37.0$	< 0.0001
	2	0.85	16.7	100	0.68	0.54	$F_{7, 141} = 17.1$	< 0.0001
Male								
Complete	1	3.53	84.7	84.7	0.88	0.13	$F_{20, 2018} = 174.0$	< 0.0001
	2	0.64	15.3	100	0.62	0.61	$F_{9, 1010} = 71.7$	< 0.0001
Random	1	4.08	75.2	75.2	0.9	0.08	$F_{20, 276} = 33.9$	< 0.0001
	2	1.35	24.8	100	0.76	0.43	$F_{9, 139} = 20.8$	< 0.0001

Table 6. Quadratic discriminant function analyses (DFA) using complete data (complete) or randomly selected records (random; n= 50 complete records/taxon) for female and male plants of *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense*: standardized correlation coefficients. Anther diameter (AD); anther distance from tip (ADT); basal diameter (BA); fruit length (FL); fruit width (FW); petal length (PL); petal width (PW); plant height (PH); staminate spike length (SSL); staminate spike width (SSW); third internode length (TIL); and, third internode width (TIW).

Character	**Female (sample/canonical)**				**Male (sample/canonical)**			
	Complete		**Random**		**Complete**		**Random**	
	1	**2**	**1**	**2**	**1**	**2**	**1**	**2**
PH	0.26	0.41	0.21	0.31	0.08	0.50	-0.02	0.68
BD	-0.04	0.00	0.04	0.16	-0.19	0.20	-0.25	0.06
TIL	-0.21	0.67	-0.29	0.87	-0.35	0.16	-0.39	0.01
TIW	0.59	-0.75	0.37	-1.03	0.90	0.09	1.11	0.1
FL	0.38	0.37	0.51	0.43				
FW	0.12	-0.51	0.09	-0.44				
SL	0.39	0.25	0.39	0.10				
SW	0.28	0.04	0.38	0.01				
SSL					-0.13	0.20	-0.09	0.23
SSW					0.86	-0.42	0.72	-0.6
AD					-0.22	0.37	-0.27	0.32
ADT					-0.42	-0.01	-0.67	0.17
PL					-0.01	0.26	0.06	0.3
PW					0.18	0.00	0.17	-0.06

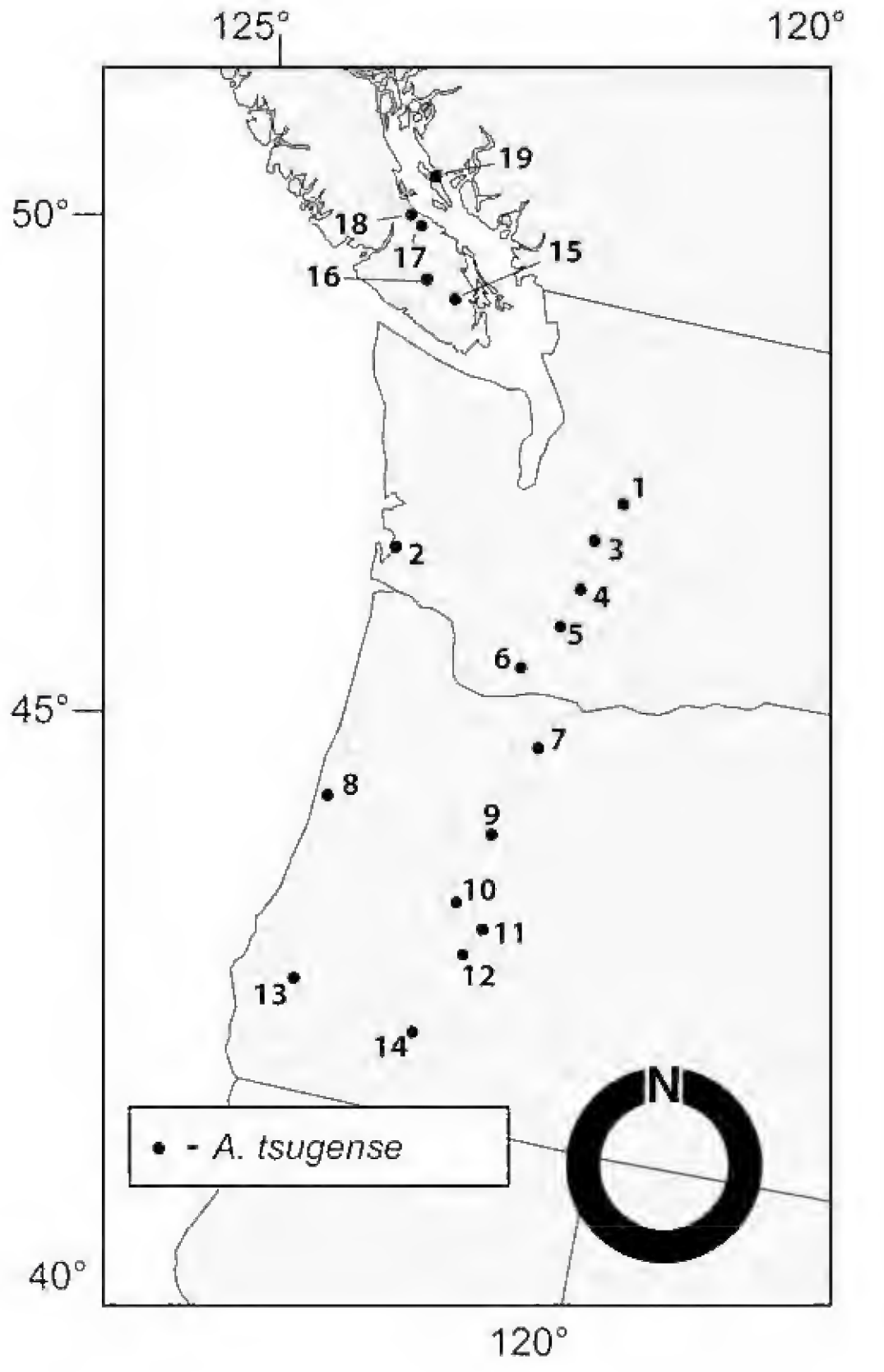

Figure 1. Approximate locations of collection sites for *Arceuthobium tsugense* in Washington, Oregon, and British Columbia. All collections on *Tsuga heterophylla*. **Washington**: **1** - Snoqualmie Pass, **2** - Westport, **3** - Huckleberry Creek, **4** - Cortright Creek, **5** - Clearwater Creek, **6** - Wind River Experimental Forest; **Oregon**: **7** - Wapinitia Pass, **8** - Desolation Saddle, **9** - Huckleberry Creek, **10** - Indigo Spring; **11** - Wall Creek, **12** - Calapooya Ridge, **13** - Union Creek, **14** - Iron Mountain; **British Columbia**: **15** - Holt Creek, **16** - Caycuse Summit, **17** - Spider Lake, **18** - Bowser, **19** -Texada Island.

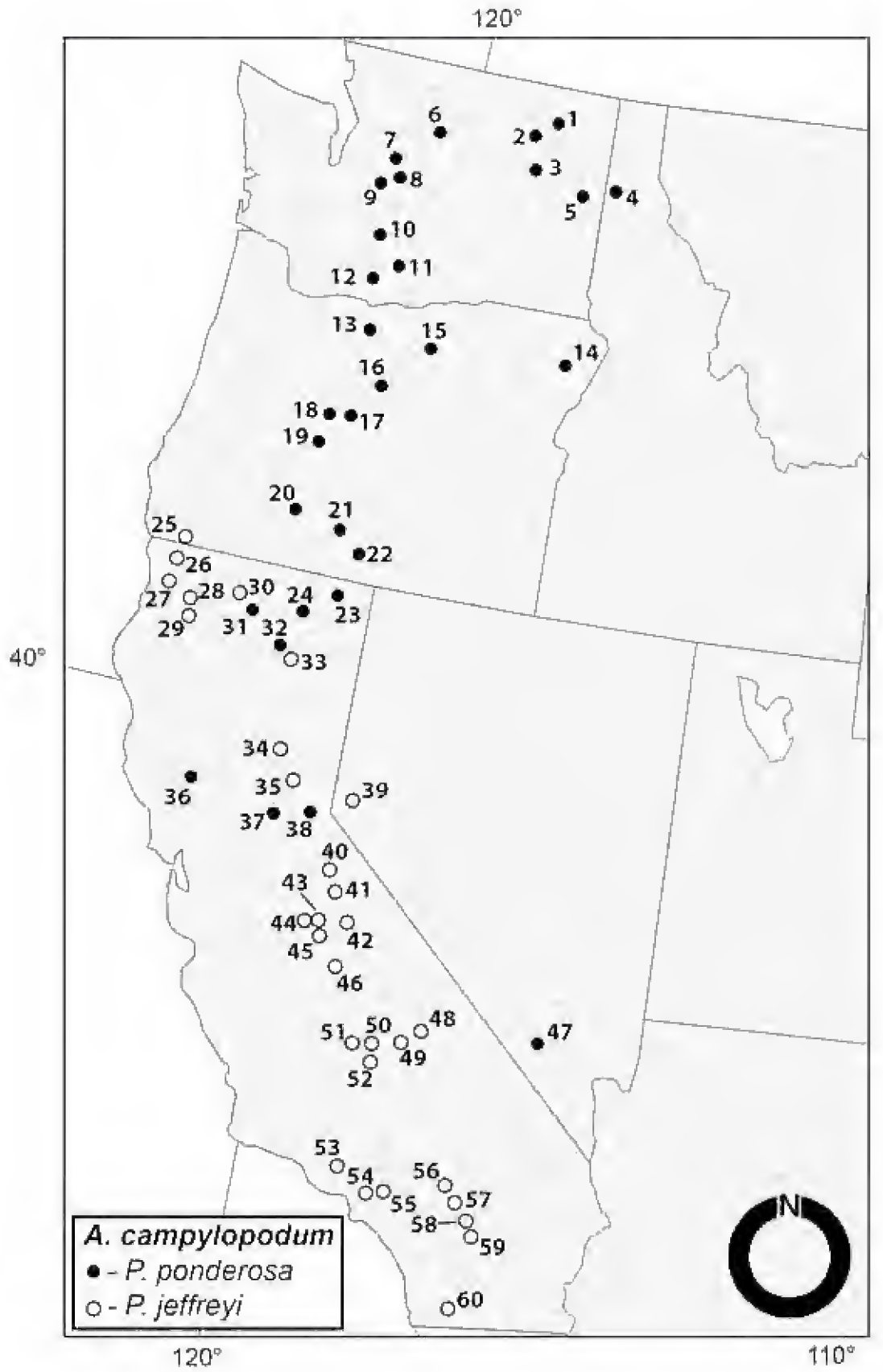

Figure 2. Approximate locations of collection sites for *Arceuthobium campylopdoum* in Washingtion, Idaho, Oregon, California, and Nevada. Closed circles present locations where plants were collected from *Pinus ponderosa*. Open circles represent locations where plants were collected from *P. jeffreyi*. Numbers correspond to the following locations: **Washington**: **1**- 4.5 km N of Gifford on St. Rte. 25, **2** - 20 km S of Fruitland on St. Rte. 25, **3** - 2 km NW of Nespelem on St. Rte. 155, **5** - 16 km S of Spokane on St. Rte. 195, **6** - 2.5 km W of St. Rte. 153 on Squaw Creek rd., **7** - Lake Wenatchee on Chiwawa River Loop rd., **8** - 2.6 km W of Squilchuck St. Park on road to Mission Ridge Ski Area, **9** - 0.8 km W of St. Rte. 97 on St. Rte 970, **10** - 17.6 km E of White Pass on St. Rte. 12, **11** - 2 km N of Satus Pass on St. Rte. 97, **12** - 3 km S of Trout Lake on St. Rte. 141; **Idaho**: **4** - 2.3 km N of Coeur d'Alene on Fernan Lake rd.; **Oregon**: **13** - 6.4 km W of Friend on forest rd. 27, **14** - 6.4 km S of Joseph on E shore of Wallowa Lk., **15** - 9.4 km on Sheep Cr. rd from forest rd. 51, Wallowa-Whitman Nat. For., **16** - 1.8 km E of Ochoco Summit on St. Rte. 26, **17** - 12.2 km W of St. Rte. 97 on St. Rte. 138, **18** - 15.2 km S of Sisters on forest rd. 16, **19** - 1 km from forest rd. 44 on forest rd. 4410, Pringle Falls Exp. For., **20** - Fort Klamath Cemetery on St. Rte. 62, **21** - 3 km W of Quartz Mtn. Pass on St. Rte. 140, **22** - Warner Mtn. Ski Hill on St. Rte. 26, **25** - 6 km S of Takilma on Greyback rd.; **California**: **23** - 3.4 km W of County rd. 48 on forest rd. 73, west shore of

Goose Lk., **24** - 16 km N of Adin on St. Rte. 299/139, **26** - 1 km S of forest rd. 17N26 on forest rd. 17N11, Klamath Nat. For., **27** - 6.2 km W of St. Rte. 96 on Dillon Mtn. rd., **28** - 9.6 km S of Callahan on St. Rte. 3, **29** - 10 km E of St. Rte 3 on forest rd. 17, Shasta-Trinity Nat. For., **30** - 2.4 km W of Stewart Hot Springs on forest rd. 17, **31** - 2 km N of St. Rte. 89 on Mt. Shasta Ski Park rd., **32** - 0.1 km S of St. Rte. 299 on St. Rte. 89, **33** - 2 km S of Old Station on St. Rte. 44, **34** - 2 km W of St. Rte. 44 on forest rd. 101, **35** - 14.4 km W of Susanville on St. Rte. 36, **36** - 19.5 km N of Upper Lake on Pillsbury Lk. rd., **37** - 7.7 km N of Pollock Pines on forest rd. 4, **38** - at entrance to Sugar Pine State Park, west shore of Lk. Tahoe, **40** - 1 km N of Markleeville on St. Rte. 89, **41** - Silver Creek Campground on St. Rte. 4, **42** - Column of the Giants on St. Rte. 108, **43** - Pinecrest Transfer Station 0.5 km W of Pinecrest on St. Rte. 108, **44** - 1 km W of Long Barn on St. Rte. 108, **45** - 8.5 km E of Crane Flat on St. Rte. 120, **46** - 2 km W of Big Creek on rd. to Shaver Lk., **48** - 8.5 km W of Sherman Pass on forest rd. 22S05, **49** - 2.2 km S of Troy Mdws. Campground, Sequoia Nat. For., **50** - 5.8 km N of rd. to Johnsonville on Western Divide Highway, **51** - Pine Flat, Sequoia Nat. For., **52** - Tiger Flat, Sequoia Nat. For., **53** - 6.2 km S of St. Rte. 33 on rd. to Mt. Reyes, **54** - 1.4 km W of Cloud Burst on St. Rte. 2, **55** - 1 km W of Big Pines on St. Rte. 2, **56** - 2.4 km N of Fawnskin on forest rd. 2N71, **57** - 1.9 km from St. Rte. 38 on rd. to Jenks Lk., **58** - near Ranger Station in Idylwild, **59** - 1.1 km S of the S Fork San Jacinto River Bridge on St. Rte. 74, **60** - 0.5 km S of Horse Heaven Campground on Sunrise Highway; **Nevada**: **39** - Bowers Mansion St. Park, **47** - 4.1 km W of Ranger Station at Old Ski Tow Historic Site, Kyle Canyon.

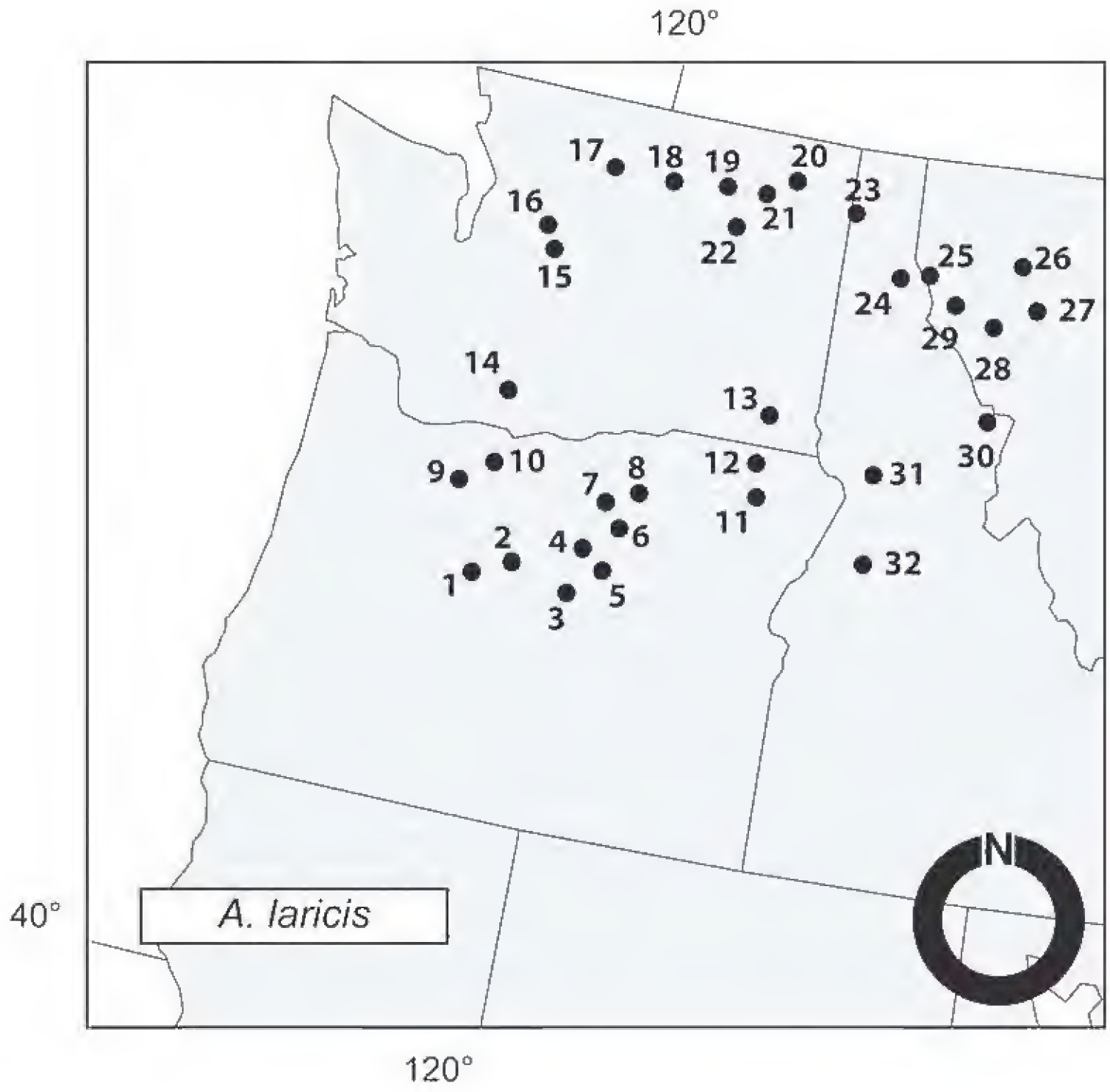

Figure 3. Approximate locations of collection sites for *A. laricis* in Washington, Oregon, Idaho, and Montana. All collections on *Larix occidentalis*. **Oregon**: **1** - Camp Sherman, **2** - Ochoco Summit, **3** - S of John Day, **4** - Blue Mountain Pass, **5** - Dixie Pass, **6** - N of Sumpter, **7** - NW of Granite, **8** - Sheep Creek, **9** - Skyline Road, **10** - Marion Point, **11** - S of Lostine, **12** - N of Enterprise; **Washington**: **13** - Fields Spring State Park, **14** - Lost Creek, **15** - Mission Ridge, **16** - S of Blewett Pass, **17** - Loup Loup Summit, **18** - Disautle Pass, **19** - Pass Creek, **20** - Tiger Meadows, **21** - S of Fruitland, **22** - E of Colville; **Idaho**: **23** - S of Coolin, **24** - Thompson Pass, **30** - W of Lolo Pass, **31** - Snow Haven Ski Area, **32** - Ponderosa State Park; **Montana**: **25** - E of Thompson Pass, **26** - S of Big Fork, **27** - E of Glacier Lake, **28** - N Valley Creek, Flathead Indian Reservation, **29** - E of Cooper Pass.

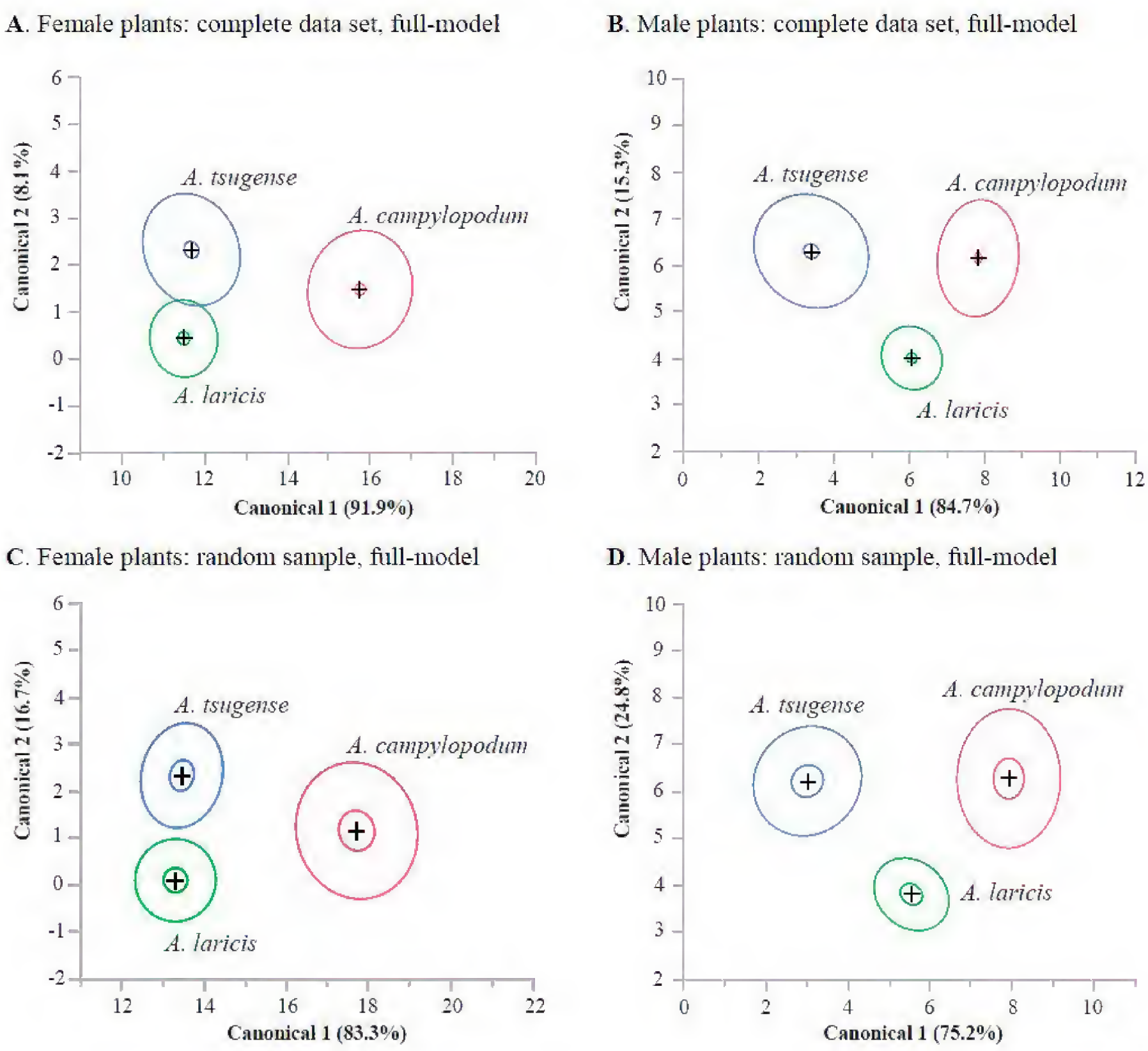

Figure 4. Canonical plots for discriminant function analyses (DFA) of *Arceuthobium campylopodum*, *A. laricis*, and *A. tsugense* based on morphological characteristics of female (A, C) and male plants (B, D) shown in Table 6. Multivariate means (crosshairs) were computed using complete data for each species by sex (A, B), whereas, to further validate the DFA, means were also calculated using a random subset (50 complete records/species) of female (C) and male plants (D), respectively. For each species (A-D), the inner ellipse correspond to a 95% confidence limit for the mean, and the outer ellipse represent a normal 50% contour illustrating the approximate area within which 50% of plants for each species reside.